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COMPLICATED ROUTES OF THE SYNHOSPITALIC PAIRS OF THE GENUS *COLOCASIOMYIA* IN JAVA, WITH DESCRIPTIONS OF TWO NEW SPECIES (DIPTERA, DROSOPHILIDAE)

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Abstract

A new synhospitalic couple of the genus *Colocasiomyia* de Meijere, *C. xanthogaster* and *C. heterodonta*, breeding in the inflorescences of the genera *Homalomena* and *Aglaonema* (Araceae) are described. New host plants of *Colocasiomyia* species are also reported with the population constitutions of the two couples in the host plants. Host preference and interspecific competition between females are also discussed.

In total 16 species of the genus *Colocasiomyia* de Meijere have hitherto been described from the area ranging from wet tropical to subtropical regions (Duda, 1923, 1924a ; Okada, 1975, 1980, 1986a, b, 1987 ; Carson & Okada, 1980 ; Toda & Okada, 1983 ; Okada & Yafuso, 1989) (Fig. 1). Of which, some synhospitalic pairs have been known to breed in the dichogamous flowers of the family Araceae (Okada, 1975, 1986a, b, 1987, 1988 ; Carson & Okada, 1980, 1982 ; Toda & Okada, 1983 ; Honda-Yafuso, 1983 ; Yafuso & Okada, 1989) (Fig. 1, shadowed species).

These flies have been known as pollinators (Carson & Okada, 1980 ; Kramadibrata & Hambali, 1983), showing modification of some morphological characters, such as bristles, adaptive to the specialized habits (Okada & Carson, 1980). The most interesting biological subjects in the *Colocasiomyia* species would, however, be the analytical approaches for the male and female reproductive success of the hermaphrodite flowers through pollination and for the mechanism that permits the complex to coexist in a host flower.

In this paper, we will describe two new species of *Colocasiomyia* associated with flowers of the genera *Homalomena* and *Aglaonema*. We also present some new data on the breeding habits of the four species of *Colocasiomyia* : *colocasiae* (Duda), *diconica* (Toda & Okada) and the two new species.

Materials and Methods

The collection and observations were made on 2-4 November, 1988 at the Bogor Botanical



Fig. 1. Distribution of the 18 species of the genus *Colocasiomyia*, shadowed : synhospitalic pairs.

Garden, Bogor, Java. When young inflorescences of the family Araceae were found, each of them was covered with gauze net to aspirate adult flies directly. Later the fly-flowers, buds, and fruits were cut and preserved individually in the plastic bag filled with 70% alcohol to return to the laboratory of the University of the Ryukyus, Japan. It was impossible to count the number of larvae of *Colocasiomyia diconica* because of the bad condition of the specimens. One adult female of a new species, *C. xanthogaster*, was dissected for examining egg morphology under binocular microscope. Some females of *C. diconica* were also dissected to examine the fecundity potential and ovoviviparity.

Results

1. Descriptions of the two new species.

Colocasiomyia xanthogaster n. sp.

Male and Female (Fig. 2A-E).

Body 1.5-1.8 mm in length. Eye (Fig. 2B) oval, dark reddish purple, bare. Second antennal joint grey, third black. Arista with 1-2 dorsal and 1 ventral long branches and a large fork. Palpus black. Ocellar triangle large, black. Frons grey, anteriorly orange grey. Periobit black. Face grey, carina large, bulbous. Clypeus grey. Cheek black, very broad, as broad as eye diameter. Anterior reclinate orbital fine. Only one long oral. Mesoscutum mat black, yellowish below. Scutellum mat black. Thoracic pleura yellowish, black below. Humerals 2, long. Acrostichal hairs in about 2 rows.

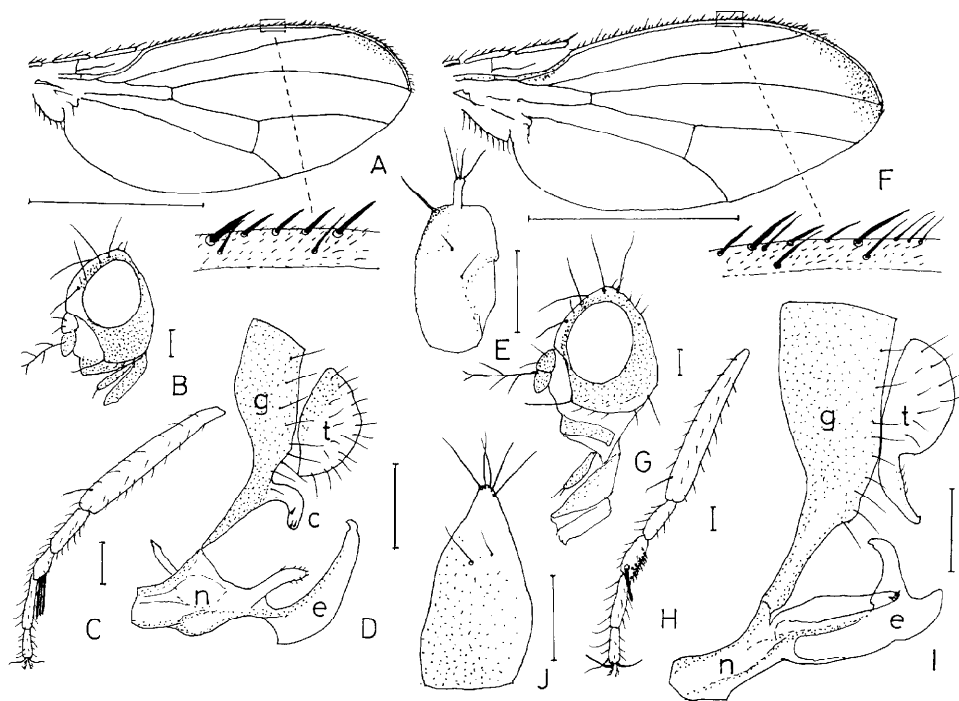


Fig. 2. A-E, *Colocasiomyia xanthogaster* ; F-J, *C. heterodonta*. A, F, wing ; B, G, head ; C, H, fore tarsi ; D, I, peripheral phallic organs ; E, J, ovipositor. c, surstylus ; e, aedeagus ; g, epandrium ; n, apodeme of aedeagus ; t, cercus.

Anterior dorsocentrals about 2/3 posteriors. Scutellars somewhat divergent, laterals 1/2 apicals. Sterno-index 1.0. Legs (Fig. 2C) yellow. $f_1 = t_{2-3}, f_{2,3} = t_{2-4}$. Second tarsal joint of fore leg apically with 3 long stout black bristles. Preapicals on all tibiae, apicals on 2nd. Wing (Fig. 2A) hyaline, apically somewhat fuscous. Costal bristles stout and thickly arranged (costal chaetotaxy type B₂). C-index 2.8, 4V-index 1.4, 4C-index 0.9, 5x-index 1.2, Ac-index 2.4, C3-fringe about 1/3. Halter yellow, knob black, rounded. Abdominal tergites yellow, thus the specific name. Male 6S without special process. Peripheral phallic organs (Fig. 2D) : genital arch narrowly elongate caudally below. Surstylus curved, with 3 sensilla. Phallic organs (Fig. 2D) : aedeagus tapering distally and clawed apically. Ovipositor (Fig. 2E) elliptical, apically with a long seta and a fringe-like hairy process.

Egg (Fig. 3A).

About 0.6-0.7 mm in length. Narrowed below the terminal disc. Terminal disc triangular, with a short filament.

Larva (Fig. 4A-C).

Estimated to be *xanthogaster*. Caudal spiracles very short, completely separated at the base. Some rows of stout spines on the body wall.

HOLOTYPE ♂, allotype ♀, 29 paratypes, Bogor, Java, 3. XI. 1988, Yafuso leg. ex flowers of *Homalomena* sp. (holotype and allotype), *H. pendula* (♀ paratype) and *Aglaonema pictum* (♀ paratype) (Araceae).

RELATIONSHIPS : This species resembles *C. toshiokai* Okada in having plumose arista, long stout bristles of male fore leg, and in the shape of ovipositor, but differs by having heavy costal bristles

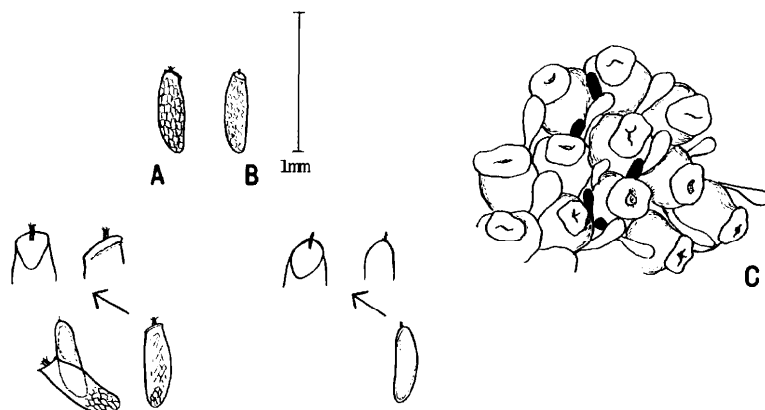


Fig. 3. A, egg of *Colocasiomyia xanthogaster*; B, egg considered to be *C. heterodonta*; C, eggs of *c. xanthogaster* deposited among the pistillate flower of *Homalomena* sp. (solid ellipse).

(costal chaetotaxy type B₂; B₀ in *C. toshiokai*), minute anterior reclinate orbital bristles, and male cercus without ventral prolongation.

DISTRIBUTION : Java.

Colocasiomyia heterodonta n. sp.

Male and female (Fig. 2F-J).

Body 1.5-2.0 mm in length. Eye (Fig. 2G) purple black, bare. Antenna black. Arista with 2 dorsal and 1 ventral long branches and a small fork. Palpus grey. Ocellar triangle mat brownish black. Frons mat brownish black. Face pale grey. Carina greyish white, bulbous. Clypeus black. Cheek black, nearly as broad as eye diameter. Anterior reclinate orbital minute. Vibrissae long, other orals fine. Mesoscutum and scutellum black, thoracic pleura yellowish white. Humerals 2, long. Acrostichal hairs in 2 rows. Anterior dorsocentrals as long as posteriors. Scutellars slightly convergent, laterals 1/3 apicals. Sterno-index about 0.5. Legs yellow, second tarsal joint of fore leg (Fig. 2H) with a long apical bristle and about 12 smaller teeth in two rows (thus the specific name). Preapicals on all tibiae, apicals on second. Wing (Fig. 2F) hyaline, apically somewhat fuscous. Costa with sparsely arranged heavy setae (costal chaetotaxy type B₂). C-index 2.0, 4V-index 1.4, 4C-index 1.0, 5x-index 1.8, Ac-index 2.4, C3-fringe 1/8. Halter black, stalk paler. Abdominal tergites black. Male 6S without special process. Periphallallic organs (Fig. 2I) : Epandrium elongate below ; surstylus triangular ; cercus narrowing ventrally. Phallic organ (Fig. 2I) : aedeagus Y-shaped. Ovipositor (Fig. 2J) conical, apically with about 4 setae.

Egg (Fig. 3B).

About 0.67 mm in length. Terminal disc round. Surface sculpture a little weak when compared to *C. xanthogaster*. Gently convex ventrally.

Larva (Fig. 4D-F).

Supposed to be *C. heterodonta*. Caudal spiracles unforked. Many rows of fine spines on the body wall.

HOLOTYPE ♂, allotype ♀, 2♂ paratypes, Bogor, Java, 3. XI. 1988, Yafuso leg. ex flowers of *Homalomena* sp. (holotype and allotype), *H. pendula* (♂ paratype) and *Aglaonema pictum* (♂ paratype) (Araceae), collected together with the foregoing species.

RELATIONSHIPS. This species resembles *C. bogneri* Okada in the arrangement of heavy bristles

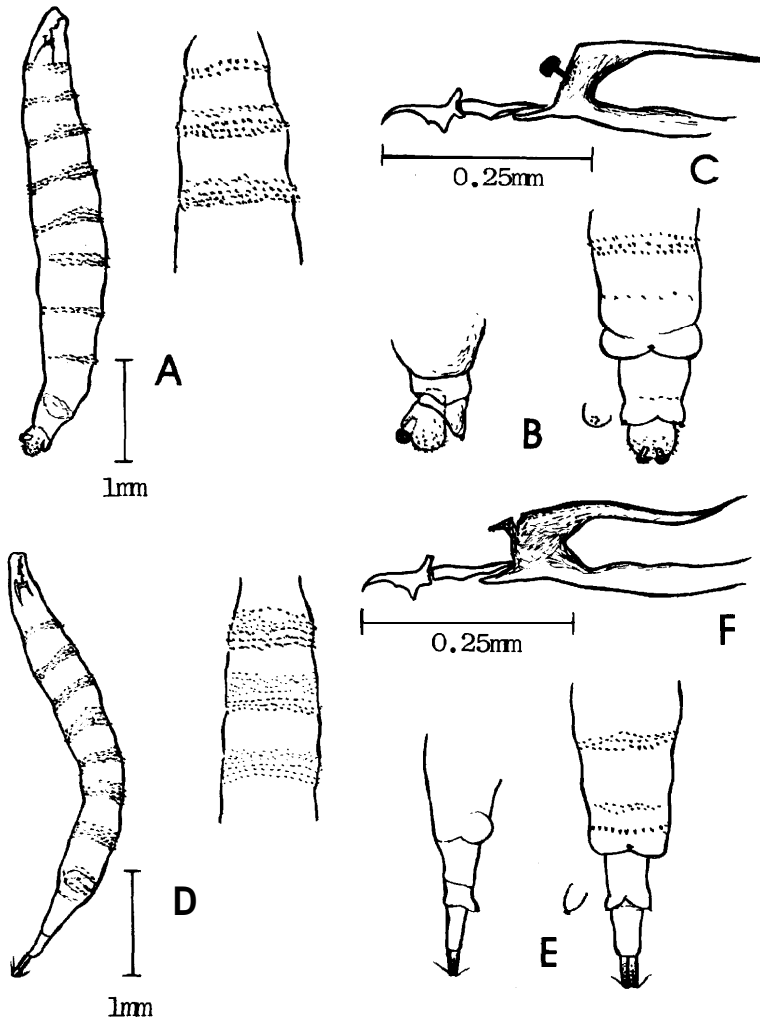


Fig. 4. Third instar larva and cephalopharyngeal skelton of *Colocasiomyia xanthogaster* (A-C) and *C. heterodonta* (D-F). A, D, lateral view (left) showing the rows of small spines on the body wall (right) ; B, caudal spiracles of *C. xanthogaster* very short, separated at the base ; E, the same of *C. heterodonta* not forked ; C, F, cephalopharyngeal skelton.

on the second tarsal joint of fore leg, but differs by having abdominal tergites yellow, wing tip cloudy, and costal setae stouter (costal chaetotaxy type $B_1; B_0$ in *bogneri*).

DISTRIBUTION : Java.

2. Host records.

Twelve flowering species of nine genera of Araceae were examined : *Homalomena pendula*, *H. sp.*, *Aglaonema pictum*, *A. nitidum*, *A. sp.*, *Xanthosoma sp.*, *Alocasia macrorrhiza*, *Colocasia gigantea*, *Diffenbachia sp.*, *Caladium bicolor*, *Monstera sp.*, and *Spathiphyllum sp.* Of which, 5 species of 4 genera were parasitized by *Colocasiomyia* species. Hitherto, *Homalomena lancifolia* from Malaysia and *H. sp.* from Philippines have been known as the host species of *Colocasiomyia*. *H. pendula* (Photo 1) and



Photo 1. *Homalomena pendula* (Bl.) Bakh f.



Photo 2. *Homalomena* sp.



Photo 3. *Aglaonema pictum* Kunth. var. *tricolor*.



Photo 4. *Colocasia gigantea* Hook. f.

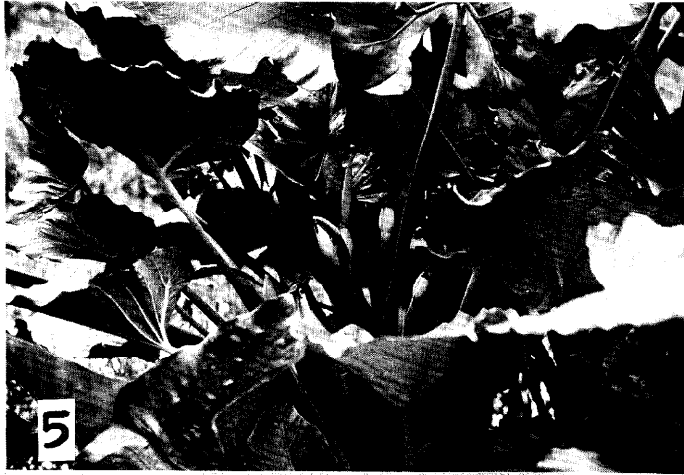


Photo 5. *Alocasia macrorrhiza* Schott.

H. sp. (Photo 2) were the host plant species of *C. xanthogaster* n. sp. and *C. heterodonta* n. sp. from Java in the present survey. *Aglaonema pictum* (Photo 3) was also recognized to rear the new couple mentioned here. The “*Homalomena* route”, named by Okada (1986a), in Java was presently known. *C. gigantea* (Photo 4) has been recorded as the host plant of *C. colocasiae* and *C. diconica* from Java (Kramadibrata & Hambali, 1983 ; Okada, 1987). *Alocasia macrorrhiza* (Photo 5) was also the host plant of the *diconica-colocasiae* couple. This synhospitalic couple parasitized *H. pendula*, too. So that, the three distribution routes of “*Homalomena* route”, “*Colocasia* route”, and “*Alocasia* route” were clarified from Java.

3. Population constitutions.

A total of 17 inflorescences of the host plants of the “*Homalomena* route” were examined, 7 of which were parasitized by the synhospitalic pair of *C. xanthogaster* and *heterodonta* (Table 1). Adult flies of the two species were collected from 3 inflorescences. They were found together habouring on the inner wall of the spathe in the shadow part of spadix (Photos 2, 3). Morphologically different types of eggs were deposited on the flower. The egg of *C. xanthogaster* was identified by dissecting an adult female. The morphology of the terminal disc and chorion surface suggests that the other type is the eggs of *C. heterodonta*. We could not confirm it by dissecting, because we had only two female specimens. Of 68 *C. xanthogaster* eggs from 6 inflorescences, 64 (94.1%) were collected from *Homalomena* flowers. Most of them were deposited in the pistillate portion. They were put individually among female flower in the spadix (Fig. 3C). Four eggs (5.9%) out of 68 were found in the inflorescence of *Aglaonema pictum*. Of 35 *heterodonta* eggs, 16 (45.7%) were found in the inflorescences of *Homalomena* sp. and 19 (54.3%) in the inflorescences of *Aglaonema pictum*. Seven eggs out of 16 were deposited on the staminate portion and 9 on the pistillate portion. The average number of eggs per female was 1.6 in *xanthogaster* (68 eggs/6 females/3 inflorescences) and 5.8 in *heterodonta* (35 eggs/2 females/3 inflorescences) (Table 1). These values suggest that *heterodonta* might have larger fecundity than *xanthogaster*. All larvae of the two species were collected in the pistillate portion of the host inflorescences. The niche segregation between them was absent.

Another synhospitalic pair of *C. diconica* and *C. colocasiae* was also sampled from the inflorescences of *C. gigantea*, *A. macrorrhiza* and *H. pendula* in Bogor. Population constitution of the pair was very different from data so far presented (Table 2). Forty two females and forty four males

Table 1. Population constitution of *Colocasiomyia xanthogaster* and *C. heterodonta* in the spadices of Araceae, Bogor, Java, 2-4 Nov., 1988.

Host No.	Host species	Stage*	Portion* .	<i>xanthogaster</i>			<i>heterodonta</i>		
				egg	larva (estimated)	adult	egg (est.)	larva (est.)	adult
11-1, 2	<i>Homalomena pendula</i>	III	P	1	6			4	
40-1	Ditto	II	[s p	9		1♂1♀			1♂
35-1	<i>Homalomena</i> sp.	I	[s p	3 2	8		1	4	
-2		I	P	2	22				
-3		II	[s p	7 40	1	2♂4♀	7 8		1♂1♀
48-1	<i>Aglaonema pictum</i>	II	—	4		1♀	19		1♀

● , developing stages : I, bud ; II, young flower ; III, staminate portion of the spadix decaying ; IV, fruit.

**, s, staminate portion ; p, pistillate portion.

—, the spadix collected on the same stem.

Table 2. Population constitution of *Colocasiomyia diconica* and *C. colocasiae* in the spadices of Araceae, Bogor, Java, 2-3 Nov., 1988.

Host No.	Host species	Stage	Portion	<i>diconica</i>			<i>colocasiae</i>		sp. c pupa
				egg	larva	pupa	adult	larva	
1-1	<i>Colocasia gigantea</i>	III	[t p	1?	8 22		1♂		
-2		II	[t p		132				
-3		III	P		38				
-4		III	P		114+				
-5		III	—		103+				
13-1	Ditto	III	—		62				
-2		II	[t p	1?	52+				
-3.4		II	—		73		44042 ♀		
25-4	<i>Colocasia macrorrhiza</i>	IV	P						5
-5		IV	P						1
-6		IV	P					1	
-9		IV	P					1	
59-1		IV	P			22			
-2		IV	P			1			
-4		IV	P			#			
-5		IV	P			it			
-6	Ditto	IV	P			10			
-8		IV	P			9			
23-1	<i>Homalomena</i>	IV	P					1	
-2	<i>pendula</i>	IV	P			3		1	

+, more.

#, many, but impossible to count because of bad condition of the specimens,

of *diconica* were aspirated from one young inflorescence of *C. gigantea*. Neither eggs nor young larvae were found here. A large number of larvae of *diconica* were obtained in other inflorescences of *C. gigantea*. They distributed from transitional region to pistillate portion in a spadix. No larva of other species was found. More than one hundred of larvae of *diconica* were also collected in the

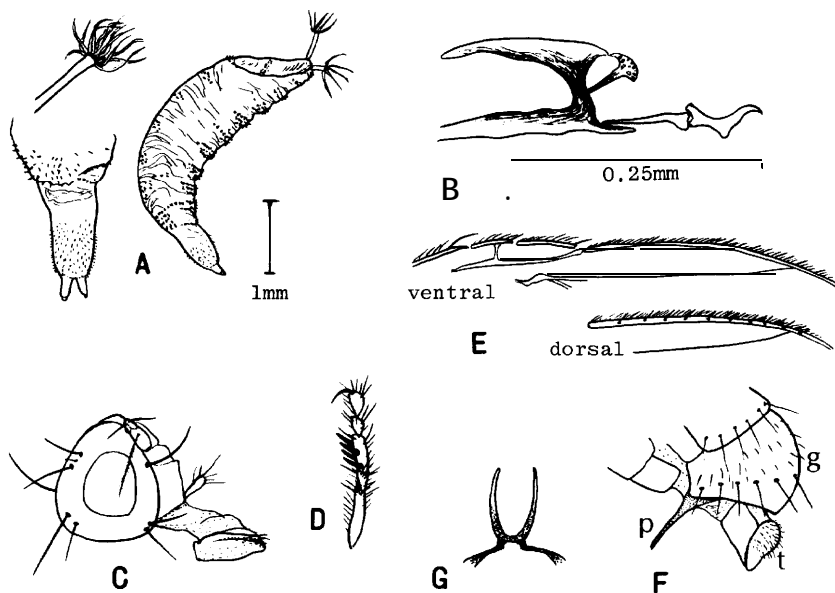


Fig. 5. *Colocasiomyia* sp. collected in the spadix of *Alocasia macrowhiza* in Stage IV. A, pupa ; B, cephalopharyngeal skelton left in the puparium ; C-G, pre-emerginal male found in the puparium. C, head ; D, fore tarsi ; E, costal chaetotaxy of fore wing ; F, periphallallic organ ; G, abdominal process of the 6th abdominal sternite. g, epandrium ; p, abdominal process of 6th sternite ; t, cercus.

Stage IV spadices of *A. mucrowhiza*. They were not together with other species as well as seen in *C. gigantea*. Forty two pupae of *diconica* were collected from 4 spadices of *A. macrowhiza* where larvae were absent. Contrary to the large number of *diconica*, the extremely small number of *colocasiae* were obtained in the Stage IV spadices of *A. macrowhiza*. They, 2 larvae, bred in the spadices where *diconica* was absent. No adult fly of *colocasiae* was caught. Eggs or pupae were also absent. Thus, *diconica* mostly occupied the spadices. The other species of the couple, *colocasiae*, did not share the habitats in *C. gigantea* and *A. macrowhiza*. One exceptional example of coexisting of the two species was seen in the *Homalomena* species. Three pupae of *diconica* and 1 larva of *colocasiae* coexisted in the Stage IV spadix of *H. pendula*. *H. pendula* was presently recorded as a common host plant species of the pair. The relationship between the two species on *H. pendula* has not yet been known.

One unknown species of *Colocasiomyia*, named for convenience sp. C in Table 2, was found from the spadices of *A. mucrowhiza*. One pupa of 6 contained an adult male in the puparium. Figure 5 showed some morphological characters of the species. We would give a new name to this species when we could get much more specimens of adults and larvae. It was also unknown whether it has a synhospitalic mate.

Discussion

From the morphological characters such as spines on the bodywall or caudal spiracles, larvae with short, separated caudal spiracles and stout spines were considered to be *xanthogaster*, and larvae with unforked caudal spiracles and fine spines to be *heterodonta*, although it was not proved by

rearing. Egg distribution in Table 1 suggested that *xanthogaster* was pistilicolous because their eggs were mostly deposited in the pistillate portion. While *heterodonta* might be stamencicolous, the half of whose eggs were found in the staminate portion. These two species might have different host preference though they parasitized the same host as a synhospitalic pair. That is, *xanthogaster* may prefer *Homalomena* species to *Aglaonema*, whereas *Aglaonema* may be favourable to *heterodonta*. A large number of eggs of *xanthogaster* on *Homalomena* may reflect their preference for *Homalomena*, and comparatively large number of eggs of *heterodonta* on *Aglaonema* suggest their preference of *Aglaonema*.

In the present survey in Bogor, the following two facts attracted our attention. The first one was that *colocasiae* was very few in number. Two larvae of *colocasiae* were hardly collected from *A. macrorrhiza* but none of them from *C. gigantea* in spite that *C. gigantea* was also the host plant of this species and it grew up nearby *A. macrorrhiza* in the Garden. The second one was that the two species, *diconica* and *colocasiae*, might not share the larval niche in a spadix. It has been reported that the two species in Burma utilized the same host spadices of *Colocasia esculenta* altogether for oviposition site or larval niche though they shared the resource microallopatrically (Toda & Okada, 1983). It was also described that many adult flies of the two species were collected simultaneously in the inflorescences of *C. gigantea* and *C. esculenta* in Java and Thailand (Okada, 1987). Contrary to this, 3 out of 4 larvae of *colocasiae* were collected in the spadices where *diconica* was absent.

These facts suggest the interspecific competition between females of the two species for oviposition site. To explain the exclusive or synhospitalic distribution of the two species in a host spadix,

Table 3. Ovarian condition of *Colocasiomyia diconica* harboured in the spadices of *Colocasia gigantea*, Bogor, 2-3 Nov., 1988, Java.

No.	No. of immature eggs		Total
	left	right	
1	2	2+1*	5
2	2	2	4
3	2	2	4
4	2	1	2
5	1+1*	2	4
6	3	1**	7
7	1	2	3
	1.9±0.7	2.1±0.7	4.1±1.6

*, mature egg containing the 1st instar larva ;

**, held in the common oviduct containing the 1st instar larva.

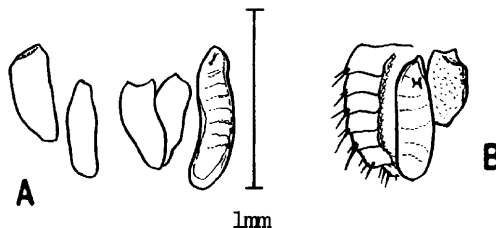


Fig. 6. Eggs of *Colocasiomyia diconica*. A, four immature eggs and one mature egg in the female specimen aspirated on the spadix of *Colocasia gigantea* ; B, a large mature egg in the female abdomen containing a full grown 1st instar larva.

the seasonal population density, host range and host preference should be examined.

Ovoviviparity, low fecundity potential and alternating development of ovariole of flower-breeding drosophilids have been reported from Taiwan (Okada, 1975), Burma (Toda & Okada, 1983), and Hawaii (Kambysellis & Heed, 1971). It was also confirmed in *diconica* in Java (Table 3, Fig. 6).

Furthermore, the spadices of *A. macrorrhiza* which produced *diconica* larvae did not contain any pupae of the species, and conversely the spadices including pupae had not larvae. This analogous situation suggests that, as well as the synhospitolic pair of Papua New Guinea (Carson & Okada, 1980), the females visited the host inflorescences for only a short time, perhaps one day. So that, the developing stage of *diconica* larvae was almost the same condition in an inflorescence. Although host plant flower provides the highly nutritious food, the restricted supply in abundance and short life span of a flower may be reflected in the short staying of these flies. They migrate to the next flower within a few days. In turn, it may be largely contribute to the allogamy of the host plant. Field observations in Okinawa suggest that *alocasiae* and *xenalocasiae* in Okinawa are strongly combined into the reproductive success of male of the hermaphrodite flower of *A. odora* (prep.). The species of *Colocasiomyia* associated with their host plants restrictedly.

Okada (1986a) estimated the three routes of synhospitolic distribution of the genus *Colocasiomyia* in relation to the host plant distribution. They are: "*Alocasia* route" in Taiwan and Okinawa; "*Homalomena* route" in Philippines and Malaysia; "*Colocasia* route" in Burma, Malaysia, Java and Papua New Guinea. In the present survey, it was confirmed that "*Homalomena* route" and "*Alocasia* route" were also present in Java in addition to the known "*Colocasia* route" (Fig. 7). Furthermore, the *colocasiae-diconica* couple covered the three routes simultaneously in one area. All of the three routes were presently confirmed in Java. "*Colocasia* route" was also found in Sulawesi (prep.) as well as the "*Alocasia* route" (Okada & Yafuso, 1989). Then, two of the three routes were

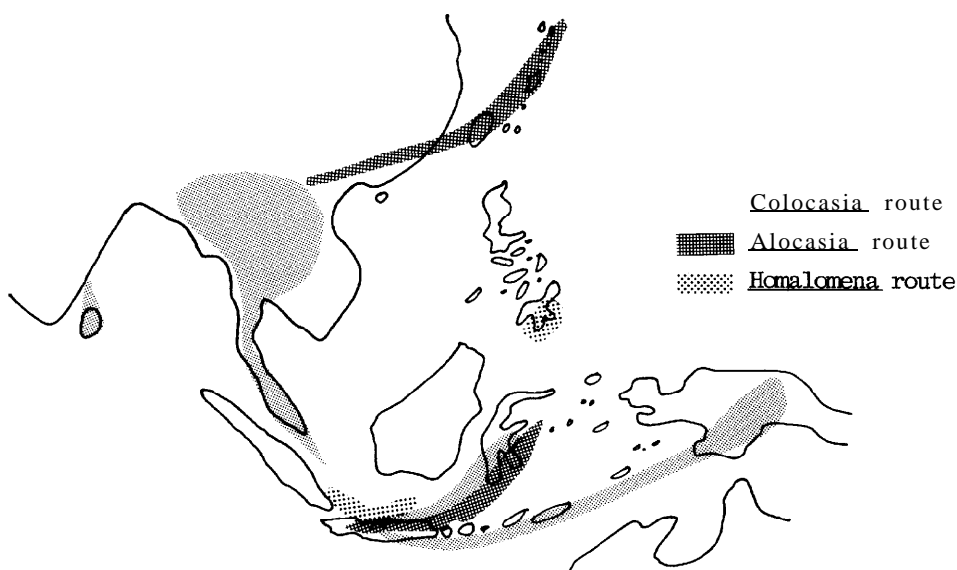


Fig. 7. Schema of the estimated host plant routes of the synhospitolic species of the genus *Colocasiomyia*, based on the hypothetical routes by Okada (1986a). The complicated routes in Java and Sulawesi were presently known.

also confirmed to be present in Sulawesi. These results indicated that the multiple *Colocasiomyia* fauna and the complicated relationship between host and synhospitalic flies would be found in Indonesia. It is predicted that many other new species or new couples of the genus should be found in this area. The old, intricate geographical history of Indonesia and the multiplicity of the fauna should greatly contribute to investigate the symbiosis and coevolution between plants and insects.

Acknowledgement

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